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Growth dynamics and genotypic variation in tropical, field-grown paddy rice (*Oryza sativa* L.) in response to increasing carbon dioxide and temperature

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Abstract

While previous studies have examined the growth and yield response of rice to continued increases in CO_2 concentration and potential increases in air temperature, little work has focused on the long-term response of tropical paddy rice (i.e. the bulk of world rice production) *in situ*, or genotypic differences among cultivars in response to increasing CO_2 and/or temperature. At the International Rice Research Institute, rice (cv IR72) was grown from germination until maturity for 4 field seasons, the 1994 and 1995 wet and the 1995 and 1996 dry seasons at three different CO_2 concentrations (ambient, ambient + 200 and ambient + 300 $\mu L\ L^{-1}$ CO_2) and two air temperatures (ambient and ambient + 4 °C) using open-top field chambers placed within a paddy site. Overall, enhanced levels of CO_2 alone resulted in significant increases in total biomass at maturity and increased seed yield with the relative degree of enhancement consistent over growing seasons across both temperatures. Enhanced levels of temperature alone resulted in decreases or no change in total biomass and decreased seed yield at maturity across both CO_2 levels. In general, simultaneous increases in air temperature as well as CO_2 concentration offset the stimulation of biomass and grain yield compared to the effect of CO_2 concentration alone. For either the 1995 wet and 1996 dry seasons, additional cultivars (N-22, NPT1 and NPT2) were grown in conjunction with IR72 at the same CO_2 and temperature treatments. Among the cultivars tested, N-22 showed the greatest relative response of both yield and biomass to increasing CO_2, while NPT2 showed no response and IR72 was intermediate. For all cultivars, however, the combination of increasing CO_2 concentration and air temperature resulted in reduced grain yield and declining harvest index compared to increased CO_2 alone. Data from these experiments indicate that (a) rice growth and yield can respond positively under tropical paddy conditions to elevated CO_2, but that simultaneous exposure to elevated temperature may negate the CO_2 response to grain yield; and, (b) sufficient intraspecific variation exists among cultivars for future selection of rice cultivars which may, potentially, convert greater amounts of CO_2 into harvestable yield.

Keywords: elevated CO_2, intraspecific variation, rice, temperature

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Introduction

Population growth, global reliance on burning fossil fuel for energy, and changes in land use practices make continuous increases in atmospheric carbon dioxide (CO_2) almost inevitable. The IPCC moderate scenarios predict that the concentration of atmospheric CO_2 will increase to ≈ 600 $\mu L\ L^{-1}$ from the current 360 $\mu L\ L^{-1}$ by the end of the 21st century (Houghton *et al.* 1996).

As atmospheric CO_2 continues to rise, there are two potential consequences with respect to plant biology. Carbon dioxide is the principle source of carbon for photosynthesis, and plants which possess the C3 photosynthetic pathway (i.e. 95% of all plant species) currently operate at suboptimal carbon dioxide levels. Increasing

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CO_2 therefore, can directly stimulate photosynthesis and subsequent plant growth (cf. Kimball 1983). A second, indirect consequence of increasing carbon dioxide level is related to its ability to trap infra-red radiation in the atmosphere (along with other so-called greenhouse trace gases) with a potential increase in global surface temperature. At present, a 2–4 °C increase in air temperature is predicted with a doubling of current CO_2 levels. Although the actual rise in global temperature is difficult to predict, any increase will affect a number of plant metabolic processes which influence photosynthesis, growth and yield.

To date, the majority of studies which have examined the photosynthetic or growth response of plants to increasing CO_2 have done so for temperate plant species for periods of one year or less in controlled environment or glasshouse facilities (see Poorter 1993; Bowes 1996 for reviews). Few long-term *in situ* studies related to the response of tropical crop or native species to increasing CO_2 concentration are available (see Hogan *et al.* 1991).

Among tropical crops, rice maintains a position of importance as a principle food source for ≈ 1.6 billion people with another 400 million depending on rice for a quarter to one half of their caloric input (Swaminathan 1984). Planted to 148 million hectares as of 1990, an estimated yield increase of 70% may be needed in the coming decades to keep pace with population demand (IRRI 1993). The large amount of land planted to rice suggests that rice may affect and be affected by climate change within the biosphere.

Several studies have examined the impact of increasing carbon dioxide and air temperature on rice growth and yield in temperate regions (see Imai *et al.* 1985; Baker *et al.* 1990; Baker *et al.* 1992; Baker & Allen 1993; Ziska & Teramura 1992). Although the response was quite variable, these studies indicate that rice, like most C3 species, can demonstrate positive increases in growth and yield with increasing CO_2 concentration; however, most studies have not examined the interaction with potential increases in air temperature. Recent field studies of tropical paddy rice (Ziska *et al.* 1997) also indicate a positive yield response of rice with increasing CO_2 concentrations, but demonstrate a lack of response of yield to CO_2 if air temperature rises concurrently. This lack of response may be related to increasing canopy temperature and subsequent infertility with simultaneous increases in CO_2 concentration and air temperature (e.g. Matsui *et al.* 1997). Phytotron studies indicated that the degree of CO_2 response varied among rice cultivars, and sufficient intraspecific variability exists so that cultivars could be selected which show a strong yield and growth response (Ziska *et al.* 1996). Similarly, variability in the response among cultivars likely also occurs for temperature. To date, however, identification of cultivars for the optimal response to CO_2 and/or temperature has not been accomplished under tropical field conditions.

In the current study, our objectives were two fold. First to examine the long-term growth and yield response of the 'standard' cultivar, IR72, to confirm earlier observations and to determine the consistency of the response over multiple growing seasons; and second, to determine vegetative or reproductive characteristics which could be used to select an optimal cultivar (i.e. one showing the maximum yield response) with increasing CO_2 concentration and/or temperature under field conditions.

Materials and methods

Field control system

All experiments were conducted using a field control system of 18 open top chambers (OTCs) located in an irrigated (paddy) field at the International Rice Research Institute (IRRI), Los Banos, Philippines (121°15′ E, 14°13′N). The OTC system was designed, constructed and operated to control both CO_2 and temperature to within + 10% of a desired setpoint 24 h a day for the duration of a given experiment. Each chamber was 2.0 m tall with an octagonal base area of 3.5 m^2 and a total volume of 7.2 m^3 including that of the extended frustrum. The extended frustrum with a 0.35 m^2 opening was attached to the top of each chamber to prevent wind intrusion and to minimize temperature fluctuations and CO_2 loss. All walls and the extended frustrum were covered with 5 mil mylar film (Dupont Corp., Wilmington, DE) that transmitted 89% of the incoming photosynthetically active radiation (PAR). Additional details concerning the operation of the system can be found in Collins *et al.* (1995) and microclimate within the chambers in Moya *et al.* 1996).

Experimental details

Each OTC was assigned one of three different CO_2 concentrations (ambient, ambient + 200 μL L^{-1}; and ambient + 300 μL L^{-1}) and one of two different air temperature levels (ambient and ambient + 4 °C). Fixed levels of elevated CO_2 were not used since ambient CO_2 can be as high as 500 μL L^{-1} at night at this field site (Ziska *et al.* 1997). All treatments (CO_2 and temperature) were maintained over a 24 h time period for each growing season from germination until maturity. Seasonal average CO_2 concentrations were 369.6 + 7.4, 570.5 + 11.6 and 664.5 + 15.7 μL L^{-1} for the 3 CO_2 treatments, (374.3 + 12.9 μL L^{-1} for open field). Seasonal average temperatures were 25.8, 29.5 and 25.6 °C for the ambient temperature, ambient temperature + 4 °C, and open field, respectively.

Additional details concerning the climate at the site can be found in Moya *et al.* 1996).

Experiments were conducted over 4 field seasons 1994 and 1995 wet season (WS, typically from early August through early November) and the 1995 and 1996 dry season (DS, typically from January through April). For each season, rice seeds were germinated in flats within each chamber at the growth CO_2/temperature treatment. At 14 d after sowing (DAS), seedlings were taken out of the flats and planted within the OTC. Hills were placed at 20 * 20 cm intervals, 3 plants per hill (i.e. 75 plants per m^2, the standard plant density for commercial production in this environment). The area surrounding the chambers was also transplanted at this time to the same density. The overall statistical design was a 2 * 3 factorial (i.e. three CO_2 treatments and two air temperatures) with three replications in a randomized block design (RBD).

IR72, a standard semidwarf cultivar, was grown for all 4 seasons. However, in the 1995 WS, 2 additional rice cultivars, IR65600–42–5–2-BSI 313, a prototype of the new plant type (NPT1, with fixed tiller production and larger panicles) and N-22 (a heat and drought tolerant rice cultivar) from India were grown with IR72 inside the OTCs to assess varietal differences in growth and yield response to increasing CO_2 and/or temperature. During the 1996 DS, another new plant type, IR65598–112–2 (NPT2) was grown together with IR72.

Crop care and management practices were standard for all seasons. Forty and 60 kg N ha^{-1} were applied basally as ammonium sulphate during each wet and dry season, respectively. After transplanting, timing of supplemental N was determined by chlorophyll meter (SPAD, model 502, Minolta Corp., Japan) measurements. The actual amount of N supplied was determined using the relationship between uptake and cumulative degree days as given by Cassman *et al.* (1994). Total amounts of N added were 110 kg N ha^{-1} in the WS and 220 kg N ha^{-1} in the DS, which came from either ammonium sulphate or urea. Differences in the amount of N to be applied between seasons are related to the light environment (see Matthews *et al.* (1995). All treatments received the same amount of N at the same time.

Growth and yield measurements

At maturity for each growing season, 22 hills ($\approx$ 1 m^2) per chamber were sampled for above ground dry matter and yield during the 1994 WS and 1995 DS. Because additional cultivars were included in the 1995 and 1996 DS, the area sampled at maturity was reduced to 0.25–0.40 m^2. This area was cut, dried and separated into vegetative (straw) and reproductive components (grain). Smaller samples (4–6 hills per chamber) were made at 36, 49 and 68 DAS as well as flowering and maturity in the 1994 WS and 1995 DS to assess growth and reproductive characteristics (Ziska *et al.* (1997). Because of limited space in the 1995 and 1996 DS, these subsamples were limited to flowering and maturity. No significant effect of increased CO_2 (or the chamber itself) on the timing of flowering was observed (Ziska *et al.* 1997). However, the high air temperature treatment resulted in consistently earlier flowering (7–10) days, irrespective of CO_2 concentration. Because of the earlier flowering times, maturity was earlier at high air temperature. In instances of earlier maturity, sampled hills were replaced by transplanting plants from outside the chamber to prevent light gaps from occurring in the canopy. These plants were not sampled at later dates.

Because of the difficulty and destructiveness of root sampling, estimates of root biomass were limited to flowering and maturity. Root biomass was determined form plants grown in 11 cm diameter, 30 cm deep PVC cylinders that were filled with soil and buried in each OTC prior to the start of the experiment. The cylinders had perforations to prevent root binding. At sampling times the cylinders were lifted from the ground and roots outside the cylinder were discarded. Soil was screened and roots gently washed with water. Roots were then oven dried and weighed to calculate root dry weight per unit ground surface area.

For each subsample plant height was measured and the number of tillers counted. Plants were then cut at ground level and separated into stems (culms) and leaf blades. Leaf area was determined photometrically with a leaf area meter (LI-3000, Li-Cor, Lincoln, NE, USA). Leaves were kept between moist paper towels to prevent leaf rolling. Dry weights were obtained separately for leaf laminae, stems (including leaf sheaths), and panicles. All plant material was oven dried at 70 °C for 72 h or until dry weights were constant. At maturity, grain yield, panicle weight, percentage filled grains and 1000 grain weight were determined in addition to vegetative parts. Sample plants for number of filled and unfilled grains were observed for two rice hills, previously tagged at flowering. Harvest index was calculated as the ratio of grain yield (at 14% moisture) to total above ground biomass. Total biomass at maturity was determined from total above ground biomass (from the larger, final sample), and estimated root weight.

Typhoons

On 3 November 1995 (i.e. 1995 WS), the experimental site was struck by a Class 3, 'super' Typhoon. The typhoon occurred after the early maturing cultivar, N-22 and the high temperature treatments for IR72 and NPT1 had been harvested; however, the ambient air temperature treatments for IR72 and NPT1 at all CO_2 concentra-

Table 1 Total dry weight (g m^{-2}) at maturity for IR72 grown at 3 different CO_2 concentrations and 2 growth temperatures for 4 field seasons. * indicates a significant difference relative to current conditions of CO_2 and temperature for a given growing season. DS = dry season; WS = wet season

[CO_2]	1994 WS	1995 DS	1995 WS[1]	1996 DS
Ambient temperature				
ambient	1216	1803	681	1892
Ambient + 200	1447*	2238*	1103*	2234*
Ambient + 300	1556*	2340*	937*	2386*
Ambient + 4 °C temperature				
Ambient	1162	1694	805	1880
Ambient + 200	1423*	2199*	1061*	1803
Ambient + 300	1492*	2343*	1070*	2059

[1]A 'Super' typhoon struck the experimental site on November 3rd prior to final maturity.

Sums of Squares

Source	d.f.	Sum of squares	Mean square	*F*-value	*P*-value
SEASON	3	16573890.2	5524630.1	243.2	.0001
CO_2	2	1891172.9	945586.5	41.6	.0001
TEMP	1	81056.8	81056.8	3.5	.0650
SEASON*CO_2	6	317900.8	52983.5	2.3	.0468
SEASON*TEMP	3	254470.5	84823.5	3.7	.0172
CO_2*TEMP	2	45467.5	22733.8	1.0	.3752
SEASON*CO_2*TEMP	6	144454.5	24075.8	1.1	.3997
Residual	48	1090588.4	22720.6		

Dependent: Total dry weight at harvest (g m^{-2})

tions experienced lodging and grain shattering. As a consequence of the typhoon, direct comparisons of yield among all 3 cultivars for that season are tentative. However, because N-22 was harvested prior to the typhoon, comparisons between this cultivar and NPT2 and IR72 regarding the relative stimulation of yield and biomass at maturity by elevated CO_2 concentration/air temperature have been made.

Data analysis

All data for IR72 were compared using a three-way ANOVA (SuperANOVA, Abacus Concepts, Berkeley, CA, USA) comparing the effects of growing season, CO_2 concentration and temperature in combination. The relative response between cultivars was also compared using a 3-way ANOVA comparing the effect of cultivars, CO_2 and temperature excluding NPT1 in the 1995 WS. Treatment effects were separated using least square means. Comparisons were made between various combinations of treatments and current conditions, i.e. the means of a treatment were compared to ambient CO_2 concentration and air temperature using a 2-way ANOVA at the 0.05 level of significance.

Results

Long-term response of IR72

Total plant biomass at maturity varied significantly as a function of growing season with dry season biomass ≈ 75% greater than wet season biomass (Table 1). Averaged across all seasons, increasing the CO_2 concentration at ambient temperature resulted in a significant increase in total biomass at maturity relative to the ambient CO_2 concentration (+ 25 and + 29% for the intermediate and high CO_2 treatments, respectively). With the exception of the 1996 DS experiment, increasing CO_2 at the elevated (i.e. + 4 °C above ambient) air temperature also resulted in a significant stimulation of total plant biomass at maturity compared to the current conditions of CO_2 concentration and air temperature. Although increased air temperature resulted in earlier maturation, no significant interaction of CO_2 concentration and temperature was observed for total biomass production during the course of the experiment (Table 1).

When examined across seasons, grain yield responded to increasing CO_2 concentration to a lesser extent than total plant biomass. Excluding the 1995 WS, grain yield increased + 16 and + 22% for the + 200 and + 300 µL

Table 2 Rice grain yield (g m^{-2}) at maturity for IR72 grown at 3 different CO_2 concentrations and 2 growth temperatures for 4 field seasons. Grain yield is reported at 14% moisture. * indicates a significant difference relative to current conditions of CO_2 and temperature for a given growing season. DS = dry season; WS = wet season

[CO_2]	1994 WS	1995 DS	1995 WS[1]	1996 DS
Ambient temperature				
Ambient	366	683	135	873
Ambient + 200	412	822*	206*	1014*
Ambient + 300	472*	850*	160	1010*
Ambient + 4 °C temperature				
Ambient	272	571	232	758
Ambient + 200	338	715	319*	641*
Ambient + 300	316	744	240	826

[1]A 'Super' typhoon struck the experimental site on November 3 prior to final maturity. Ambient temperature yields for the 1995 WS are included for comparison purposes only. See Methods for additional details.

Source	d.f.	Sum of squares	Mean square	*F*-value	*P*-value
SEASON	3	4887723.4	1629241.1	240.5	.0001
CO_2	2	110527.7	55263.8	8.2	.0009
TEMP	1	132664.0	132664.0	19.6	.0001
SEASON*CO_2	6	65212.1	10868.7	1.6	.1664
SEASON*TEMP	3	241206.5	80402.2	11.9	.0001
CO_2*TEMP	2	8843.0	4421.5	0.6	.5252
SEASON*CO_2*TEMP	6	50546.5	8424.4	1.2	.3012
Residual	48	325127.7	6773.5		

Dependent: Grain weight, 14% moisture (g m^{-2})

L^{-1} CO_2 treatments, respectively, at ambient temperature (Table 2). No difference in the degree of grain stimulation between the two elevated CO_2 treatments was observed. The 1995 WS experiment is an exception since the higher temperature treatments were harvested for grain yield prior to the typhoon while the controls were harvested after the typhoon.

Cultivar comparisons of biomass and yield

For the NPT2 cultivar, irrespective of treatment, no stimulation of either grain yield or total biomass at maturity was observed (Table 3). Rather, grain yield and biomass were adversely affected, particularly by higher air temperatures. In contrast, for the N-22 cultivar, significant stimulations of total biomass were observed for increased CO_2 levels at either growth temperature (Table 3). As with IR72, increasing CO_2 concentration stimulated grain yield (P = 0.06 for the + 200 μL L^{-1} CO_2 treatment, P = 0.008 for the + 300 treatment); however, at the higher air temperature, no significant stimulation of grain yield was observed with increasing CO_2 levels (Table 3). Three way analysis of variance, taking into account cultivar, CO_2 concentration and air temperature indicated significant variation in the cultivar*CO_2 (total dry weight, P = 0.051 and yield, P =

Table 3 Total dry weight and grain yield at maturity (g m^{-2}) for cultivars NPT2 (96 DS) and N-22 (95 WS) grown at 3 different CO_2 concentrations and 2 growth temperatures. Grain yield is reported at 14% moisture. * indicates a significant difference relative to current conditions of CO_2 and temperature for a given growing season

[CO_2]	Grain yield	Total biomass
NPT2		
Ambient temperature		
Ambient	554	1423
Ambient + 200	380*	1307
Ambient + 300	504	1547
Ambient + 4 °C temperature		
Ambient	399*	1020*
Ambient + 200	364*	1329
Ambient + 300	439	1325
N-22		
Ambient temperature		
Ambient	255	717
Ambient + 200	348	923*
Ambient + 300	401*	1139*
Ambient + 4 °C temperature		
Ambient	277	989*
Ambient + 200	191	964*
Ambient + 300	208	948*

Table 4 Statistical data (sums of squares for total dry weight and grain yield at maturity) for comparison among three rice cultivars in response to elevated CO_2 concentration and air temperature. Data are based on a comparison for years in which the greatest relative response to CO_2 and/or temperature were observed (i.e. average of 1995 and 1996 DS for IR72 1995 WS for N22 and 1996 DS for NPT2). NPT1 data were excluded due to a typhoon during harvest. Additional details are given in the Methods section

Sums of Squares

Source	d.f.	Sum of squares	Mean square	*F*-value	*P*-value
CULTIVAR	2	16214597.2	8107298.6	347.9	.0001
CO_2	2	918012.5	459006.3	19.7	.0001
TEMP	1	146575.7	146575.7	6.3	.0152
CULTIVAR*CO_2	4	228386.1	57096.5	2.5	.0510
CULTIVAR*TEMP	2	140381.1	70190.6	3.0	.0575
CO_2*TEMP	2	23257.5	11628.7	0.5	.6099
CULT.*CO_2*TEMP	4	363244.7	90811.2	3.9	.0075
Residual	54	1258481.3	23305.2		

Dependent: Total dry weight at harvest (g m^{-2})

Sums of squares

Source	d.f.	Sum of squares	Mean square	*F*-value	*P*-value
CULTIVAR	2	3596818.0	1798409.0	199.7	.0001
CO_2	2	53515.9	26758.0	3.0	.0597
TEMP	1	225356.5	225356.5	25.0	.0001
CULTIVAR*CO_2	4	78902.0	19725.5	2.2	.0823
CULTIVAR*TEMP	2	25645.1	12822.5	1.4	.2497
CO_2*TEMP	2	10180.9	5090.5	0.6	.5716
CULT.*CO_2*TEMP	4	64501.2	16125.3	1.8	.1442
Residual	54	486370.2	9006.9		

Dependent: Grain weight, 14% moisture (g m^{-2})

0.082) and cultivar*temperature (total dry weight, P = 0.057) interactions, suggesting that intraspecific variation in the response of rice to CO_2 concentration and/or temperature exists even in a small selection of cultivars (Table 4).

Because different cultivars were examined in different growing seasons, direct comparisons of absolute values are not possible. A relative comparison of total biomass and grain weight between cultivars indicated that N-22 shows the greatest relative response to CO_2 concentration (e.g. ≈ 50% stimulation of grain yield and biomass), with an intermediate response of IR72 and no response of NPT2 (Fig. 1). However, while the response of grain yield to increasing CO_2 was positive for both cultivars, no increase or a slight (nonsignificant) decrease in grain yield was observed relative to the ambient CO_2, temperature treatment if both temperature and CO_2 concentration increase simultaneously (Fig. 1).

Vegetative and reproductive characteristics in response to CO_2/temperature

Using the subsample taken at maturity, root growth appeared to be the most sensitive vegetative parameter. A consistent, positive response to increasing CO_2 concentration was observed for all 3 cultivars, with the degree of CO_2 stimulation less at elevated than at ambient temperatures (Figs 2a, 3a and 4a). Although the degree of stimulation was less overall, stem weight also showed a significant increase with increasing CO_2 for all cultivars at either growth temperature (Figs 2b, 3b and 4b). For N-22 which showed the greatest stimulation of growth with elevated CO_2 concentrations, tiller number also increased (Fig. 4c). IR72 also showed an increase in tiller number with increasing CO_2 concentrations but only at the higher air temperature (Fig. 2c). No differences in leaf area as a result of increasing CO_2/temperature were observed for any cultivar (data not shown). With respect to reproductive characteristics, only N-22 demonstrated an increase in panicle weight of individual plants at maturity in response to increasing CO_2 (at ambient air temperature) (Fig. 4d). In general, panicle weight was reduced at the higher air temperature irrespective of CO_2 concentration (significantly so for the NPT and IR72 cultivars, Figs 2d and 3d). No significant changes in percentage grain fill (Figs 2,3,4e) or 1000 grain weight (data not shown) were observed as a function of either

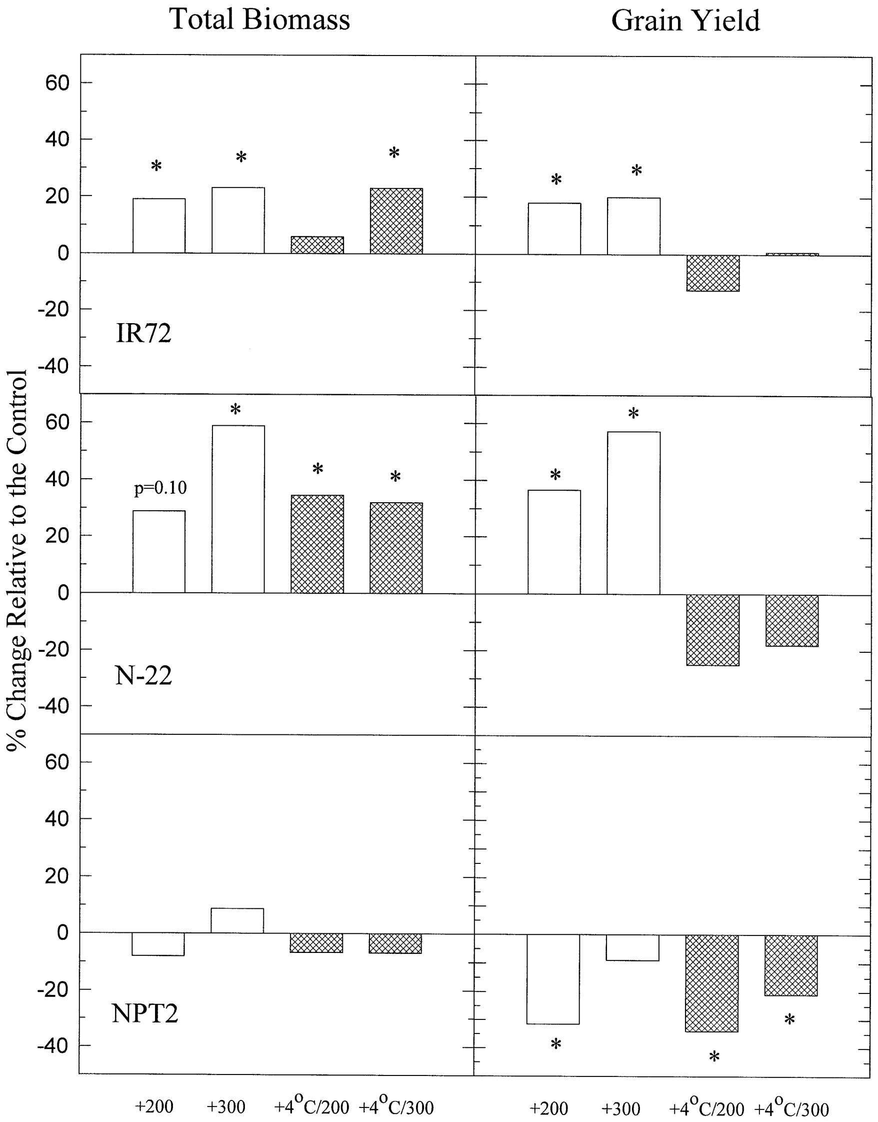

Fig. 1 Percentage change relative to the current conditions of CO_2 concentration and temperature for total biomass and grain yield at maturity for 3 rice cultivars grown at + 200 and + 300 µL L^{-1} (above ambient) CO_2 concentrations at ambient or elevated (+ 4 °C above ambient) air temperatures. Because of the 1995 WS typhoon, data for IR72 were averaged for the 1995 and 1996 DS. * indicates a significant difference at the 0.05 level relative to the ambient CO_2, air temperature control (least square means).

CO_2 concentration or air temperature. However, harvest index (i.e. the ratio of grain yield at 14% moisture to total above ground dry weight) was consistently reduced for all cultivars at the higher air temperature independently of CO_2 concentration (Figs 2,3,4f).

Discussion

The response of rice to increasing CO_2 concentration has been examined previously in a number of studies with considerable variation in the degree of stimulation (0–50% relative to current conditions of CO_2 and temperature) reported for growth and yield (cf Imai & Murata 1978; Imai *et al.* 1985; Baker *et al.* 1990, 1992). The variability may be due, in part, to differing CO_2 exposure systems and environmental conditions, as well as cultivars not representative of tropical areas. Given the reported variability, it is difficult to predict how rice might respond to elevated CO_2 or increased temperature in a tropical environment. Yet, the response of rice is of obvious importance, since most of the worlds rice production is derived from irrigated paddy rice grown in the tropics (Swaminathan 1984).

Previous work with IR72, a typical semidwarf cultivar, at this experimental site had demonstrated that at least for two field seasons, a significant stimulation in relative

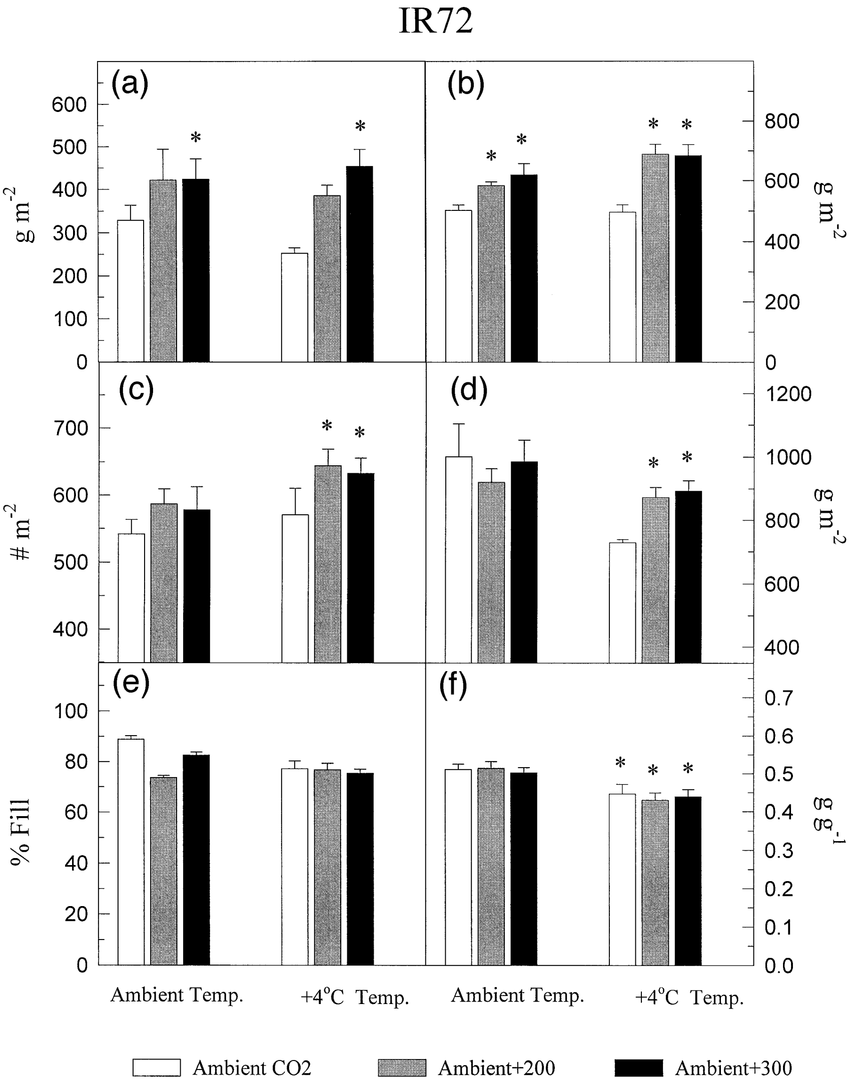

Fig. 2 Changes in vegetative or reproductive parameters for IR72 at maturity based on the 1995 and 1996 DS. (a) Root dry matter; (b) Stem weight; (c) Number of tillers per unit area; (d) Panicle weight; (e) Percent grain fill; (f) Harvest index, (ratio of grain yield at 14% moisture to above ground dry weight). * indicates a significant treatment difference relative to current conditions of temperature and CO_2 concentration at the 0.05 level (least square means). Additional details are given in Methods.

growth rate (RGR), biomass and yield was evident with increasing CO_2 concentration (Ziska *et al.* 1997). However, given the reported variability of rice from other experiments, and the potential for within and between season variability in the current study, it was felt that a multiseason data set (i.e. four seasons) was necessary to determine the relative long-term growth and yield response of rice to potential changes in CO_2 concentration and temperature. The current experiment therefore extends the earlier observations regarding the growth and yield response of IR72 and confirms that a consistent stimulation of both biomass and yield can be expected at current temperatures, across several growing seasons, as atmospheric CO_2 continues to increase (e.g. a 28% and 26% stimulation in total plant biomass at the + 300 relative to the ambient CO_2 treatment for the 1994WS and 1996 DS, respectively). In contrast to the earlier study (Ziska *et al.* 1997) no further stimulation in biomass or grain yield was observed in going from a + 200 to a + 300 $\mu L\ L^{-1}$ CO_2 concentration, which is consistent with other studies involving the CO_2 response of rice (e.g. Baker *et al.* 1990)

Given that biomass and yield are responding to increasing CO_2 concentration (with no synergism between CO_2 and temperature observed), which vegetative or reproductive components appear to show the greatest sensitivity? Which could be selected for by plant breeders seeking to optimize the yield response of rice to increasing CO_2/temperature? Earlier screening efforts of rice in the Phytotron at IRRI indicated extensive variability in the growth and yield response of rice to CO_2 concentration

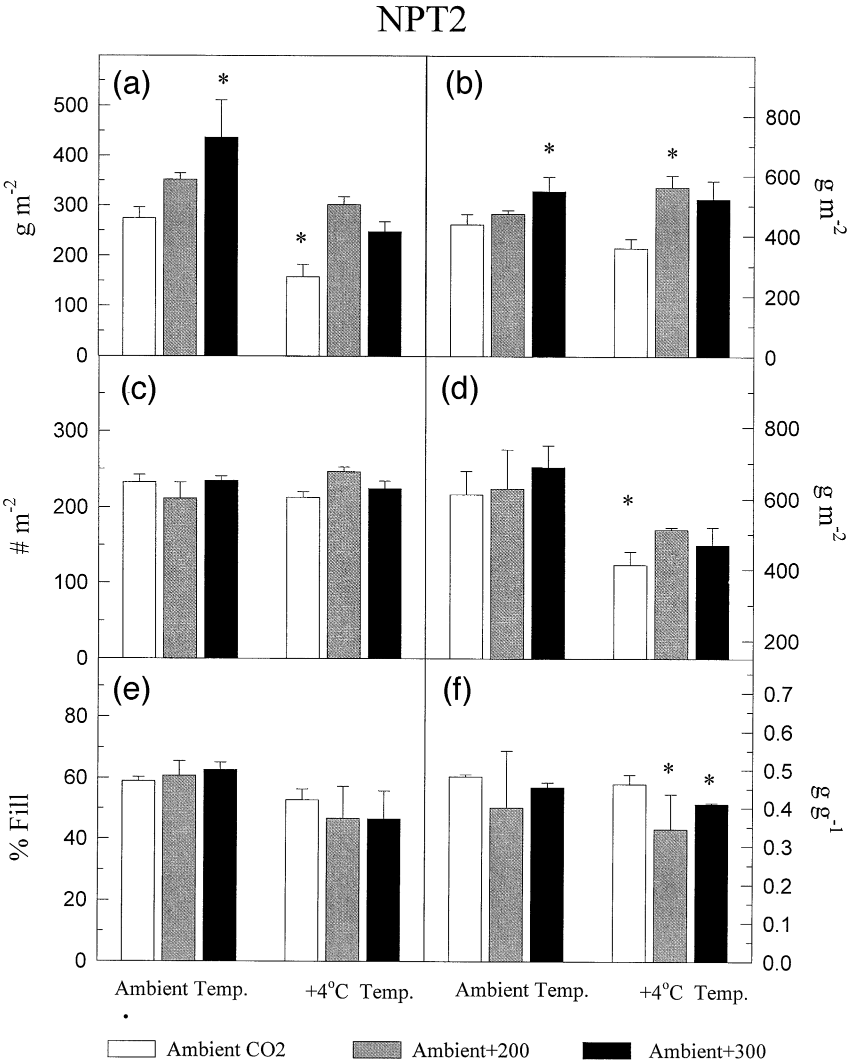

Fig. 3 Same as Fig. 2 but for NPT2 cultivar (1996 DS).

and growth temperature (Ziska *et al.* 1996). Of the cultivars tested, N-22 demonstrated the large enhancement effect with respect to growth and yield for both the Phytotron study and the current experiment even though absolute values between field and phytotron varied (Ziska *et al.* 1996).

Stimulation of root development with a subsequent increase in root dry weight at maturity appeared to be a ubiquitous response to increasing CO_2 concentration in all 3 cultivars. Roots are a principle nonphotosynthesizing sink for additional carbohydrate and the reported responses of root growth to enriched CO_2 levels have been dramatic (e.g. Rogers & Runion 1994; Prior *et al.* 1994). It has been hypothesized that any factor which inhibits root growth could decrease the relative stimulation of growth or photosynthesis with increasing CO_2 concentrations, in part because of the ratio of available sinks to sources of assimilate and the nature of feedback regulation (see Arp 1991 for a discussion). However, in the current experiment, cultivars (e.g. NPT2) which showed a significant stimulation of root growth (and a subsequent increase in root-to-shoot ratio) did not necessarily demonstrate a significant increase in total plant biomass or grain yield with increasing CO_2 concentrations.

In rice, increases in grain yield can be associated with components including: tiller number per ground area (more tillers needed to carry more panicles), increased panicle weight at maturity, seed fill and individual grain weight. For N-22, the most CO_2-responsive rice cultivar at ambient temperature, increases in grain yield with increased CO_2 concentration were associated with increases in tiller number and panicle weight. A smaller (but nonsignificant trend) for these same parameters was also observed for IR72 ($P = 0.08$ and 0.10 for tiller number and panicle weight at maturity, respectively). For the

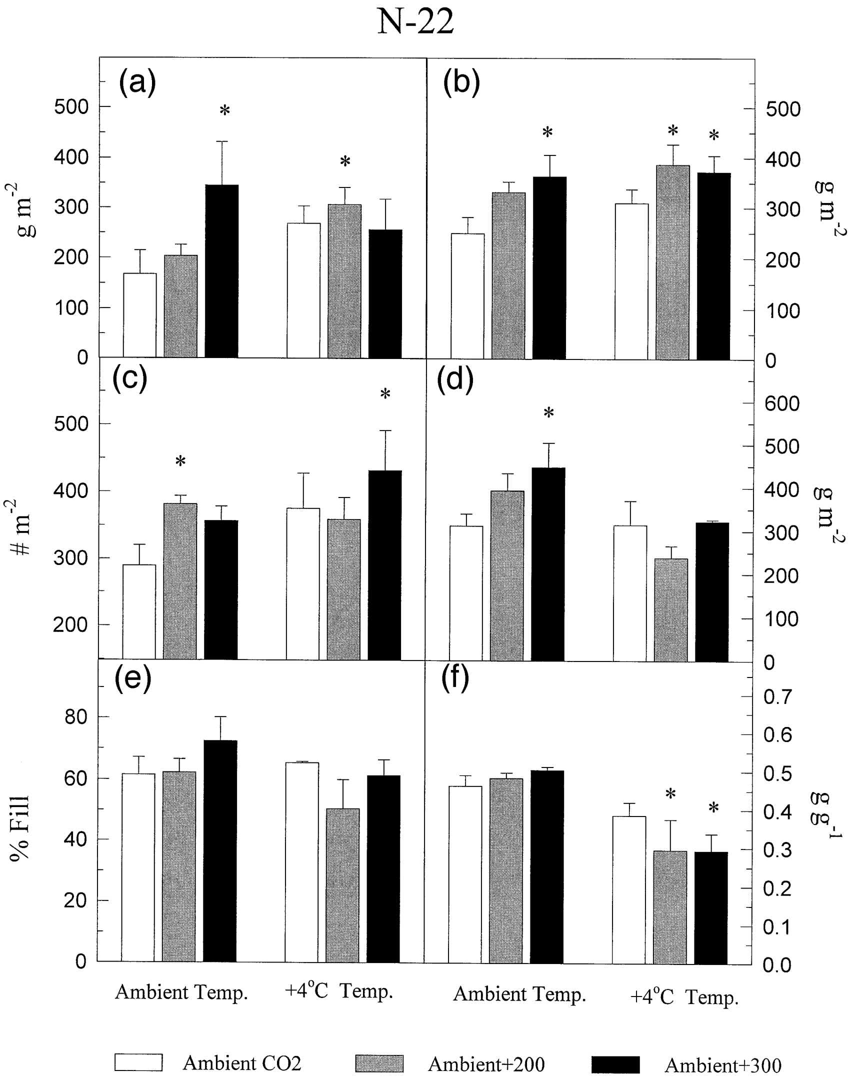

Fig. 4 Same as Fig. 2, but for the N22 cultivar (1995 WS). This cultivar matured prior to the typhoon of the 1995 WS.

NPT2 however, which had been selected for tiller uniformity in different environments, increasing CO_2 concentration had no effect on either tiller number or panicle weight. This suggests that plasticity with respect to tiller formation may be a factor in optimizing the response of rice to increasing CO_2 concentration.

In the current experiment, the positive response of rice to increasing CO_2 was uniformly negated if air temperature rose simultaneously, irrespective of cultivar. Because increasing temperature affects grain yield to a greater extent than vegetative growth, harvest index was reduced with increased CO_2 and temperature in all cultivars at all CO_2 levels. The reduction in yield with increased air temperature was associated with decreased panicle weight while other yield components were unchanged or actually increased (e.g. panicle # for IR72, Fig. 2). Reduction in panicle weight was related to spikelet fertility (Matsui *et al.* 1997).

The elevated growth temperature used in the current study (i.e. 4 °C above ambient) was at the higher end of the most recent IPCC temperature scenario predicted with a doubling of greenhouse gases (Houghton *et al.*1996). Nevertheless, since rice is grown at its upper temperature limit in many locations in Asia (see Matthews *et al.* 1995), even more moderate temperature increases (e.g. 2 °C above ambient) may be detrimental to rice fertility, especially if the projected increases in air temperature occur during the night (Ziska & Manalo 1996).

In rice it is generally agreed that a sharp decline in fertile spikelets can occur at anthesis temperatures above ≈ 31 °C (e.g. Satake & Yoshida 1978). However, previous experiments have shown that even with certain abiotic stresses (i.e. nutrients, light) increased CO_2 levels can still result in a relative stimulation of growth or yield (e.g. Hocking & Meyer 1991; Sionit *et al.* 1982). In contrast, a recent study which examined the interaction of increasing temperature and floral sterility at this experimental site during the 1995 DS showed that high temperature during flowering resulted in increased pollen sterility with the degree of sterility exacerbated if rice was exposed to simultaneous increases in CO_2 concentration and air temperature (Matsui *et al.* 1997). This unexpected interaction may be due, in part, to reduced transpiration cooling at higher air temperatures within the canopy. However, this would not explain the reduction in yield at elevated CO_2 concentration/temperature for N-22 since this cultivar flowers in the early morning and thus should avoid the higher afternoon temperatures.

Overall, it is clear that, for rice grown in the tropics, ongoing increases in atmospheric CO_2 concentration can stimulate both total vegetative biomass and grain yield. Influential model projections (reviewed in Rosenzweig & Parry 1994) have suggested that atmospheric change may threaten world food security, especially in tropical regions. However, the results presented here indicate that the actual response may be less severe, especially if the option of cultivar selction is actively pursued. Although the number of cultivars examined in this study was limited, it is evident that sufficient intraspecific variability exists under field conditions to select for rice cultivars which could have enhanced capability to convert additional atmospheric CO_2 into grain yield. Among cultivars tested in the current experiment, N-22 showed the best response with noted increases in both panicle weight and tiller number. However, if both increasing CO_2 and temperature were considered, no benefit of increasing CO_2 concentration on grain yield was realized for any of the cultivars tested. No cultivar*temperature or cultivar*CO_2 concentration effects were significant for yield, so no variation in tolerance to increased temperature was identified here. The current study re-affirms the sensitivity of rice yield to global increases in air temperature and suggests that additional resources be utilized in identifying temperature resistant cultivars which can optimize economic yield as atmospheric CO_2 concentration increases.

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References

Arp WJ (1991) Effects of source-sink relations on photosynthetic acclimation to CO_2. *Plant, Cell and Environment*, **14**, 13–20.

Baker JT, Allen LH Jr (1993) Effects of CO_2 and temperature on rice: A summary of five growing seasons. *Journal of Agricultural Meteorology*, **48,** 575–582.

Baker JT, Allen LH Jr, Boote KJ (1990) Growth and yield response of rice to carbon dioxide concentration. *Journal of Agricultural Science*, **115,** 313–320.

Baker JT, Allen LH Jr, Boote KJ (1992) Response of rice to carbon dioxide and temperature. *Agricultural Forest Meteorology*, **60,** 153–166.

Bowes G (1996) Photosynthesis and rising CO_2. In: *Photosynthesis and the Environment* (ed. Baker NR), pp. 387–407. Kluwer, The Netherlands.

Cassman KG, Kropff MJ, Zhen DY (1994) A conceptual framework for nitrogen management of irrigated rice in high-yield environments. In: *Hybrid Rice Technology: New Developments and Future Prospects* (ed. Vermani SS), pp. 81–96. IRRI Press, Manila, Philippines.

Collins L, Jones P, Ingram K, Pamplona R (1995) Open-top chambers for field studies of rice response to carbon dioxide and temperature: System design. In: *Climate Change and Rice* (Peng S, Ingram KT, Neue HU, Ziska LH eds), pp. 232–243, Springer, Berlin.

Hocking PJ, Meyer CP (1991) Carbon dioxide enrichment decreases critical nitrate and nitrogen concentrations in wheat. *Journal of Plant Nutrition*, **14,** 571–584.

Hogan KP, Smith AP, Ziska LH (1991) Potential effects of elevated CO_2 and changes in temperature on tropical plants. *Plant, Cell and Environment*, **14,** 73–778.

Houghton JT, Meira-Filho LG, Callander BA, Harris N, Kattenburg A, Maskell K (1996) *IPCC Climate Change Assessment* 1995. *The Science of Climate Change*. Cambridge University Press, Cambridge.

Imai K, Coleman DF, Yanagisawa T (1985) Increase in atmospheric partial pressure of carbon dioxide on growth and yield of rice (*Oryza sativa* L.) Japanese Journal of Crop Science, **53,** 413–418.

Imai K, Murata Y (1978) Effect of carbon dioxide concentration on growth and dry matter production of crop plants. V. Analysis of after effect of carbon dioxide treatment on apparent photosynthesis. *Japanese Journal of Crop Science*, **45,** 598–606.

IRRI (1993) *IRRI Rice Almanac* 1993–95. International Rice Research Institute, Los Banos, The Philippines, 142pp.

Kimball BA (1983) Carbon dioxide and agricultural yield: an assemblage and analysis of 430 prior observations. *Agronomy Journal*, **75,** 779–788.

Matsui T, Namuco OS, Ziska LH, Horie T (1997) Effects of high temperature and CO_2 concentration on spikelet sterility in Indica rice. *Field Crops Research*, **51,** 213–221.

Matthews RB, Kropff MJ, Bachelet D, Van Laar HH (1995) *Modeling the Impact of Climate Change on Rice Production in Asia*. CAB International, Oxford, UK, 289pp.

Moya TB, Ziska LH, Weldon C, Quilang JP, Jones P (1996) Microclimate in open-top chambers: Implications for predicting climate change effects on rice production.

Transactions of the American Society of Agricultural Engineers, **40,** 739–747.

Poorter H (1993) Interspecific variation in the growth response of plants to an elevated ambient CO_2 concentration. *Vegetatio,* **104/105,** 77–97.

Prior SA, Rogers HH, Runion GB, Mauney JR (1994) Effects of free-air enrichment on cotton root growth. *Agriculture, Forest Meteorology,* **70,** 69–86.

Rogers HH, Runion GB (1994) Plant responses to atmospheric CO_2 enrichment with emphasis on roots and the rhizosphere. *Environmental Pollution*, **83,** 155–189.

Rosenzweig C, Parry ML (1994) Potential impact of climate change on world food supply. *Nature*, **367,** 133–138.

Satake T, Yoshida S (1978) High temperature-induced sterility in Indica rices at flowering. *Japanese Journal of Crop Science*, **47,** 6–17.

Sionit N, Hellmers H, Strain BR (1982) Interaction of atmospheric CO_2 enrichment and irradiance on plant growth. *Agronomy Journal*, **74,** 721–725.

Swaminathan MS (1984) Rice. *Scientific American*, **250,** 81–93.

Ziska LH, Manalo PA (1996) Increasing night temperature can reduce seed set and potential yield of tropical rice. *Australian Journal of Plant Physiology,* **23,** 791–794.

Ziska LH, Manalo PA, Ordonez R (1996) Intraspecific variation in the response of rice (*Oryza sativa* L.) to increased CO_2: Evaluation of 17 cultivars. *Journal of Experimental Botany,* **47,** 1353–1359.

Ziska LH, Namuco OS, Moya TB, Quilang J (1997) Growth and yield response of field-grown tropical rice to increasing CO_2 and air temperature. *Agronomy Journal*, **89,** 45–53.

Ziska LH, Teramura AH (1992) CO_2 enhancement of growth and photosynthesis in rice (*Oryza sativa* L.): Modification by increased UV-B radiation. *Plant Physiology,* **99,** 473–481.